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FOSSIL DICOTYLEDONOUS WOODS FROM YELLOWSTONE NATIONAL PARK, II

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THIS PAPER is the second in a series dealing with silicified dicotyledonous woods from two regions of Yellowstone National Park, Wyoming and Montana. In the earlier paper (Wheeler, Scott, & Barghoorn, 1977), we described eight species of fossil woods in five genera (*Alnus*, *Carpinus*, *Ulmium*, *Magnoliaceoxylon*, and *Plataninium*). Species in nine additional genera are described here; other dicotyledonous woods will be described in a third paper which will include floristic and paleoecological discussions.

In Yellowstone National Park, silicified woods occur most prominently in the striking succession of fossil forests at Specimen Ridge and Amethyst Mountain along the Lamar River, and in the Gallatin area some 40 miles to the northwest in Montana. The fossil forests in both areas are in volcanoclastic rocks of the Absaroka volcanic field. The Amethyst Mountain and Specimen Ridge fossil forests are in the Lamar River Formation; the Gallatin forests are in the Sepulcher Formation. These two formations intergrade laterally and are of late early to early middle Eocene age (Smedes & Prostka, 1972). Detailed locality information was given in our first paper (Wheeler, Scott, & Barghoorn, 1977) on these fossil woods.

ANACARDIACEAE

Rhus crystallifera Wheeler, Scott, & Barghoorn, sp. nov. FIGURES 1–3.

Growth rings. Present, distinct, 1–3.5 mm. wide.

Vessel elements. Semi-ring porous, transition from earlywood to latewood gradual; extent of earlywood zone variable; pores mostly solitary and round in outline, some multiples of 2 to 3 and clusters present; tangential diameter of earlywood pores 105–205 $\mu\text{m.}$, mean 175 $\mu\text{m.}$; radial diameter of earlywood pores 118–210 $\mu\text{m.}$, mean 178 $\mu\text{m.}$; tangential diameter of latewood pores 40–100 $\mu\text{m.}$, mean 60 $\mu\text{m.}$; radial diameter of latewood pores 38–125 $\mu\text{m.}$, mean 80 $\mu\text{m.}$; length 275–460 $\mu\text{m.}$; perforation plates simple; intervacular pitting crowded alternate, to 10 $\mu\text{m.}$ across; pits to parenchyma horizontally elongate and irregular in shape; tyloses present.

Parenchyma. Paratracheal, vasicentric, generally with 4 cells per strand.

Rays. Mostly 1 to 2 cells wide, rarely 3 cells wide; heterocellular; almost all rays with inflated crystalliferous cells, in radial section these appearing twice the size of non-crystalliferous cells; multiseriate rays 6 to 27 cells, 92–600 μm . high.

Imperforate tracheary elements. Septate fibers present.

MATERIAL. One specimen of mature, silicified secondary xylem.

HOLOTYPE. U.S.G.S. Fossil Wood Collection No. D-2054A-14, measuring 70 \times 95 \times 150 mm.

LOCALITY. Amethyst Mountain, U.S.G.S. Paleobot. Loc. No. D-2054A.

Both the Anacardiaceae and Burseraceae have species with the combination of characters descriptive of this fossil; that is, pores solitary, rounded, and in radial multiples, simple perforations, vessel–ray pitting simple and variable in outline, paratracheal parenchyma, septate fibers, and narrow crystal-containing rays. The similarity of the wood anatomy of these two families is well known and is used as evidence of their close relationship (Heimsch, 1942; Webber, 1941).

The Yellowstone wood is semi-ring porous. No members of the Burseraceae are known to show any tendency to ring porosity, while ring porosity is known in the tribes Spondieae and Rhoideae of the Anacardiaceae (Heimsch, 1942). Unilaterally compound vessel–ray pitting, a feature not observed in the fossil, is a distinguishing characteristic of the Burseraceae (Brett, 1966). For these reasons, we consider the fossil to be a member of the Anacardiaceae.

Spondias axillaris Roxb. is the only member of the Spondieae in which ring porosity has been observed. We examined sections of this species and *S. mombin* L. Both have very wide rays (up to 6 to 8 cells wide), some rays have intercellular canals, and there are no more than two vessels per pore multiple. *Pistacia*, *Cotinus*, and *Schmaltzia* are ring porous members of the Rhoideae, but pore distribution and ray structure of these genera appear different than in the fossil. The anatomy of the fossil and extant species of *Rhus* is similar: the subgenus TOXICODENDRON is the only subgenus of *Rhus* reported to contain septate fibers, and septate fibers are present in the fossil (Heimsch, 1940); crystals are more common in the fossil wood than in any extant *Rhus* examined, but in all other features the fossil's anatomy is consistent with that of extant species of *Rhus*.

The numerous reports of fossil woods of the Anacardiaceae, most from Old World localities, are listed in papers by Awasthi (1965) and Kramer (1974). Fossil woods presumed to have affinities with *Rhus* have been assigned to *Rhodium* Unger (1850). Three species, *Rhodium juglandifolia* Unger, *R. ungeri* Mercklin, and *R. philippense* Orie, are known. All were described in the middle of the 19th century, a time when descriptions of fossil woods were very brief and generally unaccompanied by illustrations. Consequently, detailed comparison of the Yellowstone fossil wood with

these species is not possible. Without examination of the type material, it is also impossible to determine whether the woods called *Rhoidium* have any relationship to *Rhus* or the Anacardiaceae.

Among the oldest known woods of the Anacardiaceae are those reported from the Eocene Eden Valley, Wyoming, locality (Kruse, 1954). The two species described from this locality are quite different from the Yellowstone wood. *Schinoxylon actinoporosum* Kruse is diffuse porous and has radial chains of up to 25 pores, no axial parenchyma, and intercellular canals in the rays. This wood was said to resemble *Schinus* in those features seen in longitudinal sections; however, it does not have the distinctive ulmiform pore distribution of extant species of *Schinus*. It is unclear why this wood was assigned a name implying affinities with *Schinus*, as the Eden Valley specimen lacks the pore distinction diagnostic of this genus. The second species from Eden Valley, *Edenoxylon parviareolatum* Kruse, does not resemble any one extant genus of the Anacardiaceae. It is diffuse porous and has numerous small vessels; the rays commonly have intercellular canals. This species was subsequently reported from the lower Eocene of Herne Bay, Kent, England (Brett, 1966). These two species, a wood assigned to *Tapirira* from the Clarno beds of Oregon (Manchester, 1976), and *Anacardioxylon magniporosum* Platen (1908) from California are the only fossil woods of the Anacardiaceae known from the United States.

No Anacardiaceae are reported from the Kisinger Lakes–Tipperary flora (MacGinitie, 1974). A member of the tribe Spondieae is reported from the Golden Valley Formation, latest Paleocene age (list prepared by Hickey in Leopold & MacGinitie, 1972). *Rhus* is on a preliminary list of megafossils from the Wind River Formation, late early Eocene age (MacGinitie, 1969), and it is also reported from the Wagon Bed Formation of middle Eocene age (Leopold & MacGinitie, 1972). Two species of *Rhus* and one of *Toxicodendron* occur in the Green River flora (MacGinitie, 1969). There are two species of *Rhus* in the Florissant flora (MacGinitie, 1953).

There are 15 species in the subgenus TOXICODENDRON (Brizicky, 1962). They are mostly temperate North American and Asian in distribution, although *Rhus striata* Ruiz & Pavon grows in tropical South America.

CYRILLACEAE

Cyrilloxylon eocenicum Wheeler, Scott, & Barghoorn, sp. nov.

FIGURES 4–7.

Growth rings. Present, distinct, 2–5 mm. wide.

Vessel elements. Predominantly solitary, some pairs, angular in outline; gradually decreasing in size through the growth ring, with a tendency to form a band of pores at the beginning of the growth increment; tangential diameter of earlywood vessels 56–85 $\mu\text{m.}$, mean 70 $\mu\text{m.}$; radial diameter 67–102 $\mu\text{m.}$, mean 85 $\mu\text{m.}$; tangential diameter of latewood vessels 33–66

$\mu\text{m.}$, mean 47 $\mu\text{m.}$; 53 to 78 per square mm.; length 670–875 $\mu\text{m.}$; perforation plates scalariform, generally with more than 40 bars; intervascular pitting usually opposite but sometimes transitional and scalariform; vessel–ray pits similar to intervascular pitting.

Parenchyma. Not observed.

Rays. 1 to 7 cells wide, multiseriates with a single marginal row of square and upright cells, a few homocellular rays; multiseriates 9 to 32 cells, 164–800 $\mu\text{m.}$ high; uniseriates rare, composed of upright cells, 2 to 19 cells high.

Imperforate tracheary elements. Fiber tracheids with small bordered pits.

MATERIAL. Two specimens of mature, silicified secondary xylem.

HOLOTYPE. U.S.G.S. Fossil Wood Collection No. D-2054B-28, measuring $52 \times 68 \times 45$ mm.

LOCALITY. Specimen Ridge, U.S.G.S. Paleobot. Loc. No. D-2054B.

There are many plants which have wood with small angular vessels, scalariform perforation plates, and opposite and scalariform pitting. However, the occurrence of these structural features in combination with multiseriate rays more than three cells wide that often have a single marginal row of upright cells and rare uniseriate rays is not common. Such structural features are characteristic of the Cyrillaceae. The wood described here also resembles *Cornus*, a genus that has been reported from the Yellowstone compression flora (Dorf, 1960) and from other Tertiary floras of the Rocky Mountains (Leopold & MacGinitie, 1972). *Cornus* differs from the wood described here and from *Cyrilla* as it has numerous uniseriate rays and markedly heterocellular rays.

Slides of six specimens of *Cyrilla racemiflora* were examined. As might be expected for such a wide-ranging species (southeastern United States to the Amazon), there is considerable structural variability. Maximum ray width ranges from four to eight cells, and parenchyma abundance and distinctiveness of the growth rings varies. One specimen (Hw 19068) from the Amazon has ill-defined growth increments, while some specimens from the southeastern United States tend toward being semi-ring porous. Thomas (1960) earlier noted the absence of distinct growth rings in *Cyrilla* wood from the more tropical parts of the range of the genus. The fossils resemble those woods from the northern part of *Cyrilla*'s range as they tend toward semi-ring porosity and have distinct growth rings.

There are two other genera in the Cyrillaceae, *Purdiaea* and *Cliftonia*. *Purdiaea* (two specimens examined) differs from the Yellowstone wood as it has relatively numerous uniseriate rays. Van der Burgh (1964) and we observed that rays in *Cliftonia* have more marginal rows of square and upright cells than do rays in *Cyrilla*. The rays of the Yellowstone wood resemble *Cyrilla* more than *Cliftonia* as they generally have but a single marginal row of square and upright cells. *Cliftonia* has less parenchyma

than *Cyrilla*. The amount and distribution of parenchyma in the fossil was difficult to assess because of the relatively poor preservation. It is possible that the Yellowstone wood may resemble *Cliftonia* more than *Cyrilla* by having scanty parenchyma. Consequently, as the fossils may be intermediate in structure between these two genera, we assign them to *Cyrilloxylon*. The two specimens assigned to this taxon, D-2054B-28 and -35, differ slightly. D-2054B-35 has wider growth rings, vessel diameter does not change as much throughout the growth ring, and its vessel elements are slightly longer (up to 920 μm .), than D-2054B-28.

Fossil wood of the Cyrillaceae has been reported from the Brandon Lignite of Vermont (Spackman, 1949) and the brown coals of the Netherlands (van der Burgh 1964, 1973). The Brandon *Cyrilla* has 20 to 25 bars per perforation plate, vessel elements 550–650 μm . long, and rays up to 5 cells wide with pronounced margins of upright cells. *Cyrilloxylon europaeum* van der Burgh lacks growth rings, its perforation plates have 15 to 30 bars, and its rays are up to 5 cells wide with 1 to 7 marginal rows of upright cells. This species appears intermediate between *Cyrilla* and *Cliftonia* as the abundant parenchyma is *Cyrilla*-like, but the rays are *Cliftonia*-like.

The Cyrillaceae, a New World family of subtropical and warm-temperate areas, has three genera: *Cyrilla*, *Cliftonia*, and *Purdiaea*. *Cyrilla*, a monotypic genus, grows in acid soils along the margins of swamps and streams and in wet pinelands. In this country, it occurs in the coastal pine belt from Florida to southeast Virginia to southeast Texas; it is also present in Mexico, British Honduras, the West Indies, and northern South America. *Cliftonia* has a more restricted distribution and occurs in the Coastal Plain of Georgia, Florida, Alabama, and Mississippi. *Purdiaea* is found in Venezuela, Colombia, Peru, Cuba, and the Isle of Pines (Thomas, 1960, 1961).

There is no previous record of Cyrillaceae in the Rocky Mountains, as far as we know.

FAGACEAE

Quercinium amethystianum Wheeler, Scott, & Barghoorn, sp. nov.

FIGURES 8, 9.

Growth rings. Present, 2.5–4.5 mm. wide, not always distinct.

Vessel elements. Semi-ring porous; solitary, circular to oval in outline; in broad radial bands; tangential diameter of earlywood pores 110–200 μm ., mean 140 μm .; radial diameter 165–265 μm ., mean 225 μm .; tangential diameter of latewood 33–94 μm ., mean 64 μm .; length to 494 μm .; perforation plates simple; intervascular pitting alternate; vessel-ray pits variable, typically large, and often vertically elongate; tyloses present.

Parenchyma. Abundant, in 1- to 4-cell-wide bands, appearing wavy in cross section, particularly in the latewood; as isolated cells; and in the earlywood intermingled with tracheids forming conjunctive tissue between the vessels and rays, not swollen crystalliferous.

Rays. Rays of two distinct sizes, uniseriate (rarely biseriate), aggregate and compound; homocellular and heterocellular with marginal rows of square and upright cells, uniseriates 2 to 20 cells, 47–360 μm . high; large rays to 31 cells broad and up to 8 mm. high.

Imperforate tracheary elements. Vasicentric tracheids with pitting on radial and tangential walls, and fiber tracheids with bordered pits.

MATERIAL. One specimen of mature, silicified secondary xylem.

HOLOTYPE. U.S.G.S. Fossil Wood Collection No. D-2054A-11, measuring 41 \times 50 \times 120 mm.

LOCALITY. Amethyst Mountain, U.S.G.S. Paleobot. Loc. No. D-2054A.

Wood of certain evergreen oaks may be distinguished from deciduous oaks, as the wood of the former group is diffuse or semi-ring porous and has aggregate, rather than composite, rays in the mature wood (Williams, 1942; Brett, 1960). The wood of *Lithocarpus* is indistinguishable from the wood of such evergreen oaks. Brett (1960) emended the organ genus *Quercinium* Unger so that it would encompass species of fossil wood with evergreen oak-*Lithocarpus* structure. The specimen described here, because it is semi-ring porous, is assigned to *Quercinium*. The name *Quercocoxylon* Kräusel (1939) emend. Müller-Stoll & Mädel (1957) is also used for fossil oak woods; however, *Quercinium* has priority.

Three species of fossil oak wood have been described from the Yellowstone fossil forests: *Quercus rubida* Beyer (1954), *Quercinium knowltonii* Felix (1896), and *Q. lamarensis* Knowlton (1899). *Quercus rubida* Beyer is distinct as it is ring porous with an abrupt transition from a well-defined earlywood zone to the latewood zone, while the two species of *Quercinium* have evergreen oak-*Lithocarpus* structure.

The description of the earliest-named species, *Quercinium knowltonii* Felix, is quite brief. It was described as having oval earlywood vessels with a tangential diameter of up to 210 μm ., latewood vessels with a tangential diameter of 80–120 μm ., and parenchyma in short uniseriate bands associated with the pores. The only illustration accompanying the diagnosis of *Q. knowltonii* is a schematic drawing of a transverse section. A detailed comparison of *Q. amethystianum* with *Q. knowltonii* is not possible, but the parenchyma distribution in the two seems distinct and warrants the use of a different name for the specimen described above. An emended diagnosis of *Q. lamarensis* follows, and differences between it and *Q. amethystianum* will be discussed following that diagnosis.

***Quercinium lamarensis* Knowlton, emend. Wheeler, Scott, & Barghoorn**
FIGURES 10–12.

Growth rings. Present, 2–10 mm. wide, not always distinct.

Vessel elements. Semi-ring porous; solitary, oval in outline in earlywood, circular in outline in latewood; arranged in flamelike, radial pattern; tan-

gential diameter of earlywood pores 80–250 $\mu\text{m.}$, mean 200 $\mu\text{m.}$; radial diameter of earlywood pores 195–320 $\mu\text{m.}$, mean 240 $\mu\text{m.}$; tangential diameter of latewood pores 50–120 $\mu\text{m.}$, mean 90 $\mu\text{m.}$; length to 645 $\mu\text{m.}$; perforation plates simple; intervacular pitting alternate, pit-pairs circular in outline; vessel–ray pits large, and often vertically elongate; tyloses present, but infrequent.

Parenchyma. Predominantly apotracheal, in distinct bands 1 cell wide, at times 3 cells wide (within some growth rings these parenchyma bands more closely spaced in the earlywood), as isolated cells, and as broken uniseriate lines; also paratracheal; not swollen crystalliferous.

Rays. Rays of two distinct sizes, uniseriate (occasionally partially biseriate) and aggregate; homocellular and less frequently heterocellular with marginal rows containing some square and upright cells; uniseriates 2 to 20 cells, 64–460 $\mu\text{m.}$ high, numerous, 13–17 per mm.; aggregate rays to 1 mm. broad and 8 mm. high; units of aggregate rays, mostly 8-cell-wide rays.

Imperforate tracheary elements. Vasicentric tracheids with pitting on radial and tangential walls, and fiber tracheids with bordered pits smaller and less frequent than on the vascular tracheids.

MATERIAL. 12 specimens of mature, silicified secondary xylem.

HOLOTYPE. 2 slides: USNM 245721 a and USNM 245721 b.

LOCALITY. Specimen Ridge.

One of the most common dicotyledonous woods in the collections from Specimen Ridge is this species of *Quercinium*. We have examined sections of seven specimens collected by Scott and an additional five specimens collected by Knowlton and Read that belong to the National Museum and the U.S. Geological Survey. The original diagnosis of *Q. lamarensense* Knowlton (1899) is quite brief and is accompanied by four line drawings. All the drawings are at a fairly high magnification showing in detail a few pores, but not showing overall pore or parenchyma distribution. Quantitative data were given only for the vessels.

In his monograph on the Yellowstone fossil forests, Knowlton wrote that the material he described as *Quercinium lamarensense* came from an upright stump measuring four feet in diameter and was collected on August 22, 1887. Among Knowlton's collections housed at the National Museum, there are two slides (numbers 149 and 150) described in his notebooks as sections from an upright stump measuring four feet in diameter collected on that date. As collection data are identical and these two slides are the only ones of oaks in Knowlton's slide collection, it seems safe to assume these are the sections which Knowlton described and figured, and so we designate them the type of *Quercinium lamarensense* Knowlton, emend. Wheeler, Scott, & Barghoorn.

Knowlton acknowledged that *Quercinium lamarensense* is similar to the

earlier-described *Q. knowltonii* Felix (1896), but he suggested that the shape and size of the pores were different. It is possible that *Q. knowltonii* and *Q. lamarensense* are different names applied to the same type of wood. However, as the original material Felix described was not available for study, we are using the name *Q. lamarensense* for the woods we have examined.

Quercinium amethystianum has more parenchyma than *Q. lamarensense*, and aggregate and compound rays rather than just aggregate rays as does *Q. lamarensense*.

Ring porous oak woods are among the most commonly described fossil woods, perhaps due in part to the ease of recognizing their distinctive wood structure. Reports of fossil woods resembling evergreen oaks and *Lithocarpus* are not as numerous. Lists of the occurrence of fossil oak woods have been prepared by Prakash and Barghoorn (1961a), Müller-Stoll and Mädel (1957), and Privé (1975). There are five species of fossil wood of the evergreen oak type known from the United States, all from the Tertiary of California. Four species, *Quercinium anomalum*, *Q. solerederi*, *Q. wardii*, and *Q. lesquereuxii*, were described by Platen (1908). The fifth species, *Quercus ricardensis* Webber (1933), is from the Ricardo Pliocene. All five differ from *Quercinium amethystianum* and *Q. lamarensense* in pore size and/or parenchyma abundance.

Williams (1942) found in North American oaks a loose correlation between crystal abundance in wood and dryness of habitat: generally the dryer the habitat, the more common the crystals. Neither *Quercinium amethystianum* nor *Q. lamarensense* has crystalliferous parenchyma.

Oak leaves are abundant in the Yellowstone compression flora (Dorf, 1960, 1964). No species of *Quercus* are reported from the Kisinger Lakes-Tipperary flora (MacGinitie, 1974), but there are oaks in the older Lost Cabinian Wind River flora and the younger Green River flora.

JUGLANDACEAE

Pterocaryoxylon knowltonii Wheeler, Scott, & Barghoorn, sp. nov.

FIGURES 13–15.

Growth rings. Distinct, 5–6.5 mm. wide, visible to unaided eye, demarcated by 3 to 6 rows of flattened, thick-walled, imperforate tracheary elements.

Vessel elements. Semi-ring porous; mostly solitary or in radial multiples of 2 to 4; earlywood pores and pore multiples in diagonal arrangement; solitary pores oval in outline; latewood pores tending to be squared off, but not highly angular; tangential diameter of earlywood pores 160–310 $\mu\text{m.}$, mean 215 $\mu\text{m.}$; radial diameter of earlywood pores 225–400 $\mu\text{m.}$, mean 325 $\mu\text{m.}$; tangential diameter of latewood pores 70–140 $\mu\text{m.}$, mean 118 $\mu\text{m.}$; radial diameter 110–190 $\mu\text{m.}$, mean 165 $\mu\text{m.}$; length 460–850 $\mu\text{m.}$; perforation plates simple; intervacular pitting alternate, pits 10–12 $\mu\text{m.}$ across; vessel-ray pits not observed; tyloses present.

Parenchyma. Apotracheal, as short uniseriate lines in cross section, scanty in earlywood, more frequent in latewood with lines of greater tangential extent more closely spaced.

Rays. Multiseriates to 3 cells wide, 5 to 26 cells, 155–515 μm . high; with uniseriate margins of 1 to 8 (mostly 1 to 3) rows of square and upright cells; uniseriates 3 to 14 cells, 105–385 μm . high, cells of uniseriate rays similar in shape to uniseriate margins of multiseriate rays; 6 to 9 per mm.

Imperforate tracheary elements. Pitting not observed.

MATERIAL. One specimen of mature, silicified secondary xylem.

HOLOTYPE. U.S.G.S. Fossil Wood Collection No. D-2054B-37, measuring $35 \times 24 \times 41$ mm.

LOCALITY. Specimen Ridge, U.S.G.S. Paleobot. Loc. No. D-2054B.

The fossil resembles the wood of *Pterocarya* and *Juglans* sections CARDIACARYON (oriental butternuts) and TRACHYCARYON (*J. cinerea*, the American butternut). Wood of the black walnuts, both tropical and temperate, is distinguished by ray cell shape, the presence of crystalliferous parenchyma strands, and the reticulate thickenings in the vessel elements (Miller, 1976a, 1976b).

The rays in the fossil are three cells wide. Rays only two cells wide were observed in the five specimens of *Pterocarya rhoifolia*; three-cell-wide rays occur in *Juglans*. Kribs (1927) noted rays are only one to two cells wide in *Pterocarya*. We examined four species of *Pterocarya* in the Harvard Wood Collection and observed some occasional three-cell-wide rays in one preparation of *P. paliurus*. Müller-Stoll and Mädél (1960) reported these rays in *Pterocarya caucasia* C. A. Meyer. The three-cell-wide rays of the Yellowstone fossil are more suggestive of *Juglans* than *Pterocarya*, as such rays are rare in the former. However, there are ten species of *Pterocarya* (Willis, 1973), and examination of all species is necessary to determine if ray width is a useful feature for separating *Juglans* and *Pterocarya*.

One of the distinctive features of the fossil is the pronounced diagonal arrangement of the earlywood pores. Drs. Regis Miller and B. F. Kukachka of U.S.D.A. Forest Products examined thin-sections of the fossil and compared them to sections of *Juglans* and five specimens of *Pterocarya rhoifolia*. Drs. Miller and Kukachka did not observe diagonal pore arrangement in any extant species of *Juglans*, but did in the five specimens of *P. rhoifolia*. Diagonal pore arrangement also occurs in *P. paliurus*. Specimens of the other eight species of *Pterocarya* were not available for study. Drs. Miller and Kukachka suggest that the fossil resembles *Pterocarya* more than *Juglans*, a suggestion with which we concur.

Müller-Stoll and Mädél (1960) established the genus *Pterocaryoxylon* for juglandaceous woods with the following characteristics: diffuse or semi-ring porous; vessels thin-walled, solitary, and in radial multiples of 2 to 4;

simple perforation plates; alternate intervacular pitting; parenchyma in one-cell-wide, short, irregularly spaced bands, and 1 to 3 seriate rays. As the Yellowstone wood exhibits these characteristics common to both *Juglans* and *Pterocarya*, we are naming it as a new species of this genus.

No fossil wood resembling *Pterocarya* has been previously described from the Tertiary of North America, although *Pterocarya* is among the genera of woods listed as occurring in the Miocene Vantage, Washington, fossil forests (Beck, 1945; Prakash, 1968). Only one species of fossil wood of *Juglans* has been described from North America. *Juglans fryxellii* Prakash & Barghoorn (1961b) from the Miocene Vantage forests resembles the extant black walnuts and is distinct from *Pterocaryoxylon* as it has crystalliferous parenchyma, smaller vessels, and no diagonal pore arrangement.

To date, five species of *Pterocaryoxylon* have been described. These are *P. pannonicum* from the Pliocene of Hungary, *P. honshouense* (originally called *Pterocarya rhoifolia* by Watari in 1952), *P. chinense* from the Tertiary of China, *P. pilinyense* from the Tertiary (Helvetian) of Hungary, and *P. subpannonicum* from the Pliocene of France (Privé, 1974). *Pterocaryoxylon honshouense* and *P. chinense* both have rays only 1 to 2 cells wide. *Pterocaryoxylon honshouense* also is characterized by pores in diagonals and so appears structurally similar to *Pterocarya*. *Pterocaryoxylon pilinyense* Greguss also has 1- to 2-cell-wide rays, but it has crystalliferous parenchyma, a feature not associated with *Pterocarya* or the butternuts. *Pterocaryoxylon pannonicum* and *P. subpannonicum* have rays to 3 cells wide, but do not show any evidence of diagonal pore arrangement. Woods assigned other generic names, but which might be transferred to *Pterocaryoxylon* include *Juglandinium caucasicum* Gaivoronsky from the Oligocene of the U.S.S.R., *J. tasseewii* Naschokin from the Tertiary of the U.S.S.R., and *Juglandoxylon* sp. Petrescu & Nuta from the Miocene of Rumania (Privé, 1974).

Both *Juglans* and *Pterocarya* are members of the Kisinger Lakes flora (MacGinitie, 1974), and both occur at many Tertiary localities in the Rocky Mountains. The history of *Pterocarya* in the Rocky Mountain region was summarized by Leopold and MacGinitie (1972).

MYRICACEAE

Myrica absarokensis Wheeler, Scott, & Barghoorn, sp. nov.

FIGURES 16–19.

Growth rings. Present, distinct.

Vessel elements. Diffuse porous; predominantly solitary, some pairs; tangential diameter 30–85 μm . (mean 50 μm .); radial diameter 47–118 μm ., mean 75 μm .; 65–110 per square mm.; length 505–735 μm .; perforation plates all scalariform with 7 to 16 bars; intervacular pitting predominantly opposite, some transitional, vessel-ray pits similar to intervacular pitting.

Parenchyma. Apotracheal diffuse, as isolated strands, often inflated and crystalliferous.

Rays. Multiseriate to 4 cells wide; 4 to 25 cells, 80–600 μm . high; with uniseriate margins of 1 to 9 rows of square and upright cells; uniseriate 2 to 8 cells, 92–350 μm . high, apparently composed of only square and upright cells; 8 to 12 per mm.

Imperforate tracheary elements. Fibers with bordered pits on both radial and tangential walls.

MATERIAL. Five specimens of mature secondary xylem.

HOLOTYPE. U.S.G.S. Fossil Wood Collection No. D-2054B-11, measuring 75 \times 59 \times 50 mm.

LOCALITY. Specimen Ridge, U.S.G.S. Paleobot. Loc. No. D-2054B.

There are five specimens assigned to this taxon (D2054B-11, -21, -23, -25, and -34). There is some variation in quantitative characters, particularly vessel density, but this sort of variation is not considered taxonomically significant. The minimum tangential diameter of a vessel element is 32 μm . in all specimens, the maximum tangential diameter varies from 60 to 87 μm ., the mean varies from 46 to 57 μm .; vessel density ranges from 50 to 200 per square mm.; and the number of bars per perforation plate ranges from 6 to 20, although in all specimens it is most frequently 12. Vessel elements up to 1200 μm . long occur in some specimens.

The combination of characters of these woods (small solitary vessels, scalariform perforation plates, opposite intervascular pitting, and apotracheal diffuse parenchyma) occurs in many unrelated families, of which only four have an average vessel element length of less than 800 μm . These are the Hamamelidaceae, Cornaceae, Cyrillaceae, and Myricaceae.

In the Hamamelidaceae, vessel-ray pitting is typically large and elongate, and intervascular pitting is predominantly scalariform. The wood of the Cyrillaceae is characterized by perforation plates of 30 to 50 bars and few uniseriate rays; that of the Cornaceae, by perforation plates with many (more than 20) bars, multiseriate rays frequently higher than 1 mm., and no crystalliferous parenchyma. Metcalfe and Chalk (1950) report that *Kaliphora* and *Torricellia* have simple perforations, but Willis (1973) places *Torricellia* in its own family and notes that *Kaliphora*, which is indigenous to Madagascar, should probably be excluded from the Cornaceae. As the Yellowstone woods have small vessel-ray pitting, opposite intervascular pitting, less than 20 bars per perforation plate, low rays, and inflated crystalliferous parenchyma strands, they differ from members of these families. The structural features of these woods match those of the Myricaceae, and they are assigned to that family.

Slides of the wood of eight species of *Myrica* were examined. Of these species, the Yellowstone woods most closely resemble *M. cerifera* and *M. rubra*, as both have inflated crystalliferous axial parenchyma and predominantly scalariform perforation plates. Some species of *Myrica* do have

mostly or exclusively simple perforation plates and lack crystalliferous parenchyma.

Myricoxylon hungaricum Müller-Stoll & Mädel (1962) from the Miocene of Hungary differs from the Yellowstone wood as this Hungarian fossil wood lacks growth rings and has predominantly simple perforation plates and a higher ray density. Müller-Stoll and Mädel also noted the structural similarity of *Myrica* wood to wood of the Cornaceae and Hamamelidaceae and used number of bars per perforation plate and nature of vessel to ray parenchyma pitting to distinguish between these families.

Kruse (1954) described an Eocene fossil wood and referred it to the genus *Myrica*. This wood from Eden Valley, Wyoming, was described as having perforations with up to 35 to 40 bars, a larger number of bars than is characteristic of the extant Myricaceae. We prepared new sections of the type of *Myrica scalariformis* Kruse and observed the number of bars per perforation plate to range from 15 to 32, most commonly numbering 20 to 22 bars. This is more consistent with the anatomy of extant *Myrica* species. *Myrica scalariformis* differs from the Yellowstone wood as there are more bars per perforation plate, no crystalliferous axial parenchyma, a lower vessel density, and enlarged cells in the rays and the axial parenchyma. We did not observe enlarged parenchyma cells in any of the extant species of *Myrica* we examined, and such cells are not mentioned in descriptions of the anatomy of the family (Metcalf & Chalk, 1950; Record & Hess, 1943). It is possible that the Eden Valley wood has been incorrectly assigned to *Myrica*.

There are numerous reports of putative *Myrica* leaves from Cretaceous and early Tertiary localities in North America. Chourey (1974) examined these reports in detail and found that most of these fossils cannot be considered to be *Myrica*. Identification of a leaf as *Myrica* requires use of venation pattern, leaf morphology, and cuticular features. As most of the putative *Myrica* species are represented by specimens that are either fragmentary, poorly preserved, or without cuticle, it is not possible to determine their affinities. Chourey suggests that, to date, there have been only eight occurrences of megafossils which are probably Myricaceae. Berry described many *Myrica* leaves from the Eocene of southeastern United States. His collections and new collections from this area were examined with especial care, but no *Myrica* leaves were found in either the original collections or the new ones.

Pollen of the Myricaceae is reported from a few North American Tertiary localities. According to Chourey, “. . . not until Eocene times is the family Myricaceae well established . . . The limited record of *Myrica* pollen, however, might also show a more authentic record of the evolution and distribution of *Myrica* throughout the Cretaceous and Tertiary than is indicated by common overuse of the generic name for fossil leaves.” Wolfe (1973) noted that the history of the family is uncertain as its pollen is similar to other amentiferous families.

The Yellowstone wood represents one of the oldest occurrences of the family and the genus. It has primitive wood structure for the genus as it

has exclusively scalariform perforation plates.

Today *Myrica* has a nearly cosmopolitan distribution, but does not occur naturally in northern Africa, central and southeastern Europe, Australia, and southwest Asia (Willis, 1973). *Myrica cerifera*, a species which occupies a wide variety of habitats, has a remarkably wide range and grows in the southeastern United States, the larger islands of the West Indies, and parts of Mexico and Central America. *Myrica rubra* is a member of the mixed mesophytic and evergreen sclerophyllous broad-leaved forest associations of China (Wang, 1961).

NYSSACEAE

Nyssa saximontana Wheeler, Scott, & Barghoorn, sp. nov.

FIGURES 20–23.

Growth rings. Present, distinct, 2–5.5 mm. wide.

Vessel elements. Diffuse porous; solitary and in radial multiples of 2 to 4, and in radial chains with a single fiber separating the vessels; tangential diameter 55–110 μm ., mean 83 μm .; radial diameter 60–115 μm ., mean 97 μm .; 35–57 per square mm.; length 700–1400 μm .; perforation plates scalariform with more than 20 bars; intervascular pitting opposite to transitional, pits often square or rectangular in outline; vessel–ray pitting similar to intervascular pitting.

Parenchyma. Seen only in longitudinal sections as isolated strands, apparently apotracheal diffuse.

Rays. Multiseriate to 2 (rarely 4) cells wide; 8 to 32 cells, 440–1500 μm . high, markedly heterocellular with 1 to 18 marginal rows of square and upright cells; some rays composite with uniseriate bridges between multiseriate portions of ray; uniseriate 1 to 10 cells, 155–679 μm . high; 8 to 11 per mm.

Imperforate tracheary elements. Pitting not observed.

MATERIAL. One specimen of mature secondary xylem.

HOLOTYPE. U.S.G.S. Fossil Wood Collection No. D-2054B-41 measuring 34 \times 22 \times 35 mm.

LOCALITY. Specimen Ridge, U.S.G.S. Paleobot. Loc. No. D-2054B.

According to van der Burgh (1964, p. 285), crowded opposite intervascular pits which are somewhat squared in outline are diagnostic of *Nyssa*. This type of pitting occurs in the fossil. The combination of characters of the fossil is diagnostic of the Nyssaceae as determined by a survey of the descriptions of the wood anatomy of different families (Metcalfe & Chalk, 1950). There is also some resemblance to *Ilex*. A few species of *Ilex* do have crowded opposite pits which are square in outline. In most species of *Ilex* there are fewer rows of marginal upright cells, and

the rays are generally wider. One of the characteristics of the fossil is vertical fusion of rays; this feature is found in *Nyssa* (Record & Hess, 1943; and personal observation) and is rare in *Ilex*. Slides of the wood of both *Nyssa* and *Ilex* and the descriptions of *Ilex* species in Baas's (1973) publication were compared with the Yellowstone wood. Wood of *Nyssa javanica* (Hw 16849) and *Nyssa sinensis* (Hw 21459) agrees in every detail with wood of the fossil. Vessel element distribution, density, and size; pitting type; ray structure; and parenchyma distribution are identical.

The genus *Nyssoxylon* was established for those woods resembling *Nyssa* and *Davidia*. *Camptotheca* can be distinguished from these two genera as it has perforation plates with less than 20 bars and very few pore multiples. *Nyssa* and *Davidia* closely resemble one another structurally. Comparing the two genera, Metcalfe and Chalk (1950) found that *Davidia* tends to have a larger number of bars per perforation plate, more scalariform pitting, less parenchyma, a higher ray density, and fibers with more conspicuously bordered pits than *Nyssa*. We examined two slides of *D. involucrata* and found that the vessels were more angular and there were fewer pore multiples than were found in the fossil.

Five species of fossil woods whose affinities are suggested to be with *Nyssa* have been described. These are: *Nyssoxylon japonicum* Mädel (1959) from the Tertiary of Japan; *Nyssa eydei* Prakash & Barghoorn (1961b) from the Miocene of Washington; *Nyssoxylon haanradense* van der Burgh (1964) from the Netherlands brown coal; *N. romanicum* Petrescu (1970) from the Oligocene of Rumania; and *N. ishikariense* Suzuki (1975) from the Eocene of Japan. *Nyssoxylon japonicum* differs from the Yellowstone wood as the former has a higher vessel density, a greater number of bars per perforation plate, and rays only up to two cells wide. *Nyssa eydei* is distinguished from the Yellowstone wood as the former has a lower vessel density, more parenchyma, longer vessel elements, taller rays, a higher ray density, and crystalliferous parenchyma. *Nyssoxylon haanradense* is represented by one poorly preserved specimen, and the features seen in cross section are not described; unlike the Yellowstone wood, however, it does have numerous crystalliferous parenchyma strands and its rays are rarely three cells wide. The most recently described species, *N. ishikariense* Suzuki, has smaller vessels, a higher vessel density, and narrower and more frequent rays than the Yellowstone wood.

Fruits, leaves, and/or pollen of *Nyssa* have been reported from localities in Europe, Asia, and North America ranging in age from Paleocene to Pliocene (Eyde & Barghoorn, 1963). Most of the leaves from North American sites have been compared to the extant species of eastern North America, particularly the *Nyssa sylvatica* complex. Some of the fruits, notably *Nyssa brandoniana* Eyde & Barghoorn (1963) and *Paleonyssa spatulata* Scott (1954), seem more closely to resemble *Nyssa javanica* (Eyde & Barghoorn, 1963). Brown (1962) listed two species of *Nyssa* leaves at a number of Paleocene localities in the Rocky Mountains and

High Plains. A *Nyssa* fruit resembling the extant *N. ogeche* was reported from the Metzel Ranch flora of Montana (Becker, 1972).

At present, *Nyssa* is native to eastern North America and eastern Asia, with *N. sylvatica* occurring in Mexico at altitudes of 3000 to 5000 feet (Eyde, 1963). *Nyssa sinensis* grows in the mixed mesophytic forest and evergreen oak forests of China (Wang, 1961).

ROSACEAE

***Prunus gummosa* (Platen) Wheeler, Scott, & Barghoorn, comb. nov.**
FIGURES 24–27.

Pruninium gummosum Platen, Naturf. Gesell. Leipzig Sitzungsber. 34: 122–127. 1908.

Growth rings. Present, distinct, 1–7 mm. wide.

Vessel elements. Diffuse porous; solitary, in clusters, or in radial multiples of 2 to 4; tangential diameter 32–74 $\mu\text{m.}$, mean 47 $\mu\text{m.}$; radial diameter of solitary pores 78–98 $\mu\text{m.}$, mean 90 $\mu\text{m.}$; length to 370 $\mu\text{m.}$; spiral thickenings commonly present; perforation plates simple; intervascular pitting alternate, minute to small, pit-pairs round, rarely touching; vessel-ray pits similar to intervascular pitting; tyloses occasionally present.

Parenchyma. Very rare, as isolated strands, generally of 4 cells, seen only in longitudinal sections, apparently apotracheal diffuse.

Rays. Multiseriates to 4 cells wide; 5 to 44 cells, 105–763 $\mu\text{m.}$ high; with uniseriate margins of 1 to 6 (most frequently 1 to 2) rows of square and upright cells; uniseriates 1 to 10 cells, 46–285 $\mu\text{m.}$ high, some composed entirely of square and upright cells, others with some procumbent cells, in tangential section cells of uniseriate rays oval in outline; 8–17 per mm.

Imperforate tracheary elements. Fibers with circular bordered pits on both radial and tangential walls, pits approximately 5 $\mu\text{m.}$ across.

Gum ducts. Traumatic vertical gum ducts present, often in tangential groups at beginning of growth increment.

MATERIAL. One specimen, D-2054A-21, of mature secondary xylem, measuring 63 \times 71 \times 41 mm.

LOCALITY. Amethyst Mountain, U.S.G.S. Paleobot. Loc. No. D-2054A.

The combination of characters of this fossil (small vessels, small to minute alternate intervascular pitting, prominent spiral thickenings, and traumatic vertical canals) is diagnostic of the Rosaceae, exclusive of the Chrysobalanoideae. Pore multiples are characteristic of the Prunoideae (Metcalf & Chalk, 1950), and *Prunus* is particularly prone to the formation of traumatic vertical canals (Jane, 1970; Panshin & DeZeeuw, 1970; Record & Hess, 1943). As pore multiples and vertical canals are present.

the specimen is assigned to the Prunoideae. Vertical canals also occur in *Laurocerasus* of the Prunoideae, and this genus (a segregate of *Prunus*) is similar anatomically to *Prunus*. *Laurocerasus* may be distinguished from *Prunus* as, in the former, rays frequently have four or more marginal rows and parenchyma is vasicentric (Metcalf & Chalk, 1950). The Yellowstone wood resembles *Prunus* as it has sparse diffuse parenchyma and generally less than four marginal rows of ray cells.

Pruninium gummosum from Amethyst Mountain was described by Platen in 1908. The differences between his diagnosis and the specimen described here are slight. The quantitative data are nearly identical: according to Platen, maximum tangential diameter is 75 $\mu\text{m.}$, we found it to be 74 $\mu\text{m.}$; he described rays as up to 50 cells high, we found a maximum height of 44 cells. We did not observe any scalariform perforation plates, although he noted their rare occurrence. The diagnosis of *Pruninium gummosum* is so close to the specimen we studied that it almost seems as if we had fragments from the same stump. There is less variation than may be observed in wood taken from different portions of the same tree. We consider *Pruninium gummosum* Platen and the specimen described here to be conspecific, and their anatomies are indistinguishable from species of the extant genus *Prunus*. As discussed in the first paper on Yellowstone fossil dicotyledonous woods, it is not required that species of fossil wood be assigned to organ genera when their anatomical features are those of a single modern genus and such an assignment obscures the contributions of paleobotany to the history of a genus. Consequently, we hereby transfer the species *Pruninium gummosum* Platen to *Prunus* and make the new combination *Prunus gummosa* (Platen) Wheeler, Scott, & Barghoorn.

Reports of fossil woods of the Rosaceae exclusive of the Chrysobalanoideae are few. *Prunus* (?) (*Beck 1673*) is on a list of woods of the Miocene Vantage fossil forests (Beck, 1945). Thin-sections of this wood (*Beck 1673*, HPC 56667) were examined. This specimen appears to be *Ulmus pacifica* Prakash & Barghoorn (1961a) rather than *Prunus*. There are no other descriptions of fossil wood of the Prunoideae. Fossil woods assigned to the Rosaceae include *Lyonothamnoxylon* Page (1964) from the Pliocene of Nevada, *Rosaceoxylon* Shilkina (1958) from the late Tertiary of Russia, *Maloidoxylon* from the Tertiary of France (Grambast-Fessard, 1966) and the Miocene of Colorado (Wheeler & Matten, 1977), and *Pomoxylon* Hofmann (1944). The last is not a valid name as no species name was assigned nor was a species described when the genus was first named.

Prunus is a cosmopolitan genus of some 430 species (Willis, 1973). Baas (1973) has found that spiral thickenings are characteristic of the temperate members of the genus. Spiral thickenings are prominent in the specimen described here.

Both megafossils and microfossils of *Prunus* occur in the Kisinger Lakes-Tipperary flora. MacGinitie (1974) considered the leaves similar to those of the extant *Prunus serotina* Ehrlich. Species of *Prunus* have also been described from Florissant (MacGinitie, 1953) and the Green River flora

(MacGinitie, 1969), and reported from the older Wind River flora (MacGinitie, 1969).

STAPHYLEACEAE

Turpinia lamarensis Wheeler, Scott, & Barghoorn, sp. nov.

FIGURES 28–32.

Growth rings. Indistinct.

Vessel elements. Solitary and in radial multiples of 2 to 8, mostly 2 to 4; square to rectangular in outline; tangential diameter 55–115 μm ., mean 85 μm .; radial diameter 78–155 μm ., mean 124 μm .; 14 to 22 per square mm.; length .76–1.47 mm.; perforation plates exclusively scalariform with 26 to 51 bars; intervascular pitting subopposite, opposite, and transitional, often scalariform at ends of vessel elements; vessel–ray pits similar to intervascular pitting.

Parenchyma. Exact distribution not determinable, isolated strands seen in longitudinal section, some adjacent to vessel elements.

Rays. Multiseriate to 4 cells wide, occasionally 5 cells wide; 11 to 37 cells, 415–2440 μm . high; markedly heterocellular with uniseriate margins of up to 16 rows of upright and square cells; vertical ray fusions; uniseriate 2 to 25 cells, 127–1840 μm . high, apparently composed of only square and upright cells; occasionally crystals in slightly enlarged ray cells; 7 to 10 per mm.

Imperforate elements. Some fibers with bordered pits.

MATERIAL. One specimen of mature, silicified secondary xylem.

HOLOTYPE. U.S.G.S. Fossil Wood Collection No. D-2054B-24, measuring 77 \times 27 \times 93 mm.

LOCALITY. Specimen Ridge, U.S.G.S. Paleobot. Loc. No. D-2054B.

Small vessels that are both solitary and in radial multiples, opposite intervascular pitting, vessel–ray pitting that is round to elongate, exclusively scalariform perforation plates with more than 20 bars, average vessel element length greater than 800 μm ., markedly heterocellular rays, and sparse parenchyma are all diagnostic of the Staphyleaceae. The fossil somewhat resembles members of the Styracaceae, but in this family perforation plates generally have fewer than 20 bars, and the vessel–ray pitting is very fine. *Turpinia* is the only genus in the Staphyleaceae with pores in radial multiples and more than ten rows of marginal upright cells, so the fossil is assigned to this genus.

According to Willis (1973), *Turpinia* is a genus comprised of 30 to 40 species occurring from Ceylon to Japan, Malaysia, and Central and tropical South America. We examined only six of the species. The Old World species examined have predominantly solitary vessels, a fairly high vessel

density, thick-walled fibers, and elongate vessel-ray pitting. The New World species examined have numerous radial multiples, a relatively low vessel density, thin-walled fibers, and vessel-ray pits that have a round outline and are not as coarse as those of the Old World species. The structural features of *Turpinia absarokensis* are more consistent with those of the New World species of the genus, at least those available to us for comparison.

The Kisinger Lakes flora (MacGinitie, 1974) does not contain any members of the Staphyleaceae. *Turpinia* appears on a preliminary generic list of the Lost Cabinian Wind River flora of late early Eocene age (MacGinitie, 1969), but we know of no other reports of the genus in the Tertiary of the Rocky Mountains nor of any reports of fossil wood of *Turpinia*. Fossil seeds of *Turpinia* have recently been recognized in the Oligocene Brandon Lignite of Vermont (Tiffney, 1977). The Brandon *Turpinia uliginosa* most closely resembles the New World representatives of the genus. Tiffney based this comparison on the examination of 20 extant species.

ULMACEAE

Zelkovoxylon occidentale Wheeler, Scott, & Barghoorn, sp. nov.

FIGURES 33–37.

Growth rings. Distinct.

Vessel elements. Semi-ring porous; transition from earlywood to latewood gradual; tangential diameter of earlywood vessels 83–124 μm ., mean 112 μm .; radial diameter 125–190 μm ., mean 165 μm .; solitary and in radial multiples of 2 to 4, circular to oval in outline; latewood vessels tangential diameter 36–70 μm ., mean 50 μm ., in clusters of 3 to 20 cells and more rarely in radial multiples of 2 to 6, often tending to form tangential or oblique bands; perforation plates simple; intervacular pitting crowded alternate, hexagonal in outline due to crowding; spiral thickenings in the smaller elements.

Parenchyma. Paratracheal, vasicentric, or not completely ensheathing vessels or vessel clusters, most commonly 4 cells per strand.

Rays. Multiseriate to 4 (rarely 5) cells wide, 9 to 52 cells, 170–860 μm . high; with 1 to 3 marginal rows of square and upright cells, frequently inflated crystalliferous cells in marginal rows and along side of rays, some homocellular rays also; uniseriate rays few, low, 1 to 4 cells high.

Imperforate tracheary elements. Libriform fibers and vascular tracheids, vascular tracheids with spiral thickenings and crowded alternate pits, generally associated with small vessel elements.

MATERIAL. One specimen of mature, silicified secondary xylem.

HOLOTYPE. U.S.G.S. Fossil Wood Collection No. D-2054B-26, measuring 44 \times 34 \times 41 mm.

LOCALITY. Specimen Ridge, U.S.G.S. Paleobot. Loc. No. D-2054B.

The structural features of this fossil, particularly latewood pore distribution and spiral thickenings in the smaller tracheary elements, clearly indicate its affinities with the Ulmaceae. Genera in the Ulmaceae with some degree of ring porosity and heterocellular rays are *Celtis*, *Zelkova*, and *Hemiptelea*. *Hemiptelea* is readily distinguishable as it has scalariform perforation plates, few radial multiples, and storied vessels. The Yellowstone wood shares features with both *Zelkova* and *Celtis*. Inflated crystaliferous ray cells are characteristic of *Zelkova*. Ray cells of *Celtis* often contain crystals, but the cells are not enlarged as they are in *Zelkova* and the fossil. Rays in *Celtis* are predominantly heterocellular; those in *Zelkova* are predominantly homocellular. Wood of extant *Zelkova* species is strictly ring porous, the transition from earlywood to latewood is very abrupt, and there is a distinct band of large earlywood pores. Radial multiples are very rare in *Zelkova*, occurring in only 0 to 8 percent of the pores (Sweitzer, 1971).

Celtis is an anatomically diverse genus with both diffuse and ring porous species. The abruptness of the transition from earlywood to latewood may vary within a species, probably reflecting differences in habitat. Five of six specimens of *C. occidentalis* had an abrupt transition from earlywood to latewood, while one was semi-ring porous with a gradual transition in size and distribution of the pores. Sweitzer (1971) studied three specimens of *Planera*: two were diffuse porous, the third ring porous. The arrangement of the pores, in addition to the size, differs between ring and diffuse porous species: radial multiples are common in the diffuse porous species of *Celtis*, rare in ring porous species.

Sweitzer (1971) suggested that ring porosity and spirals should be considered as specializations in Ulmaceae which are correlated with a seasonal temperate environment. Cox (1941) studied species of *Celtis* from temperate and tropical regions and concluded that species of tropical zones are diffuse porous and lack spiral thickenings, while those of temperate regions are ring porous and have spiral thickenings. Spiral thickenings are present in the small tracheary elements of the Yellowstone fossil and it is intermediate in the development of the ring porous condition.

The earliest known ring porous woods are Eocene (Chowdhury, 1964). The known early Eocene floras of North America indicate that rainfall was evenly distributed throughout the year. MacGinitie (1974) suggested that by the early middle Eocene, the climate of the Rocky Mountains was seasonal. The development of ring porosity may be correlated with the advent of a seasonal climate.

The fossil wood described here resembles *Celtis* as both have similar pore distribution, but the fossil wood has a character (inflated ray cells) that occurs only in *Zelkova*, a genus with ring porous wood.

Celtis is not common in the fossil record of the Rocky Mountains, while *Zelkova* is common. *Celtis mccoshii* Lesquereux is one of the least common fossils in the Eocene Green River flora and is also rare in the Oligocene Florissant flora (MacGinitie, 1969, 1953). *Zelkova* is a member of the Kisinger Lakes flora (MacGinitie, 1974). One may speculate that this

wood might represent wood of a tree which had foliage recognizable as *Zelkova*, but whose wood had not yet developed the presumably derived ring porous condition. The wood does share more features with *Celtis* than with *Zelkova*, and it is difficult to assess how much weight should be attached to a single distinctive feature, such as these enlarged ray cells.

A fossil wood that is very similar to the Yellowstone wood is *Zelkovoxylon dacicum* Petrescu (1971) from the Oligocene of Rumania. It has very inflated crystalliferous ray cells, like extant *Zelkova* and the Yellowstone specimen. It also has vessels in radial multiples, heterocellular rays, and is semi-ring porous, all features present in the Yellowstone wood, but which neither Sweitzer nor we found to be characteristic of *Zelkova*. Petrescu seems to have weighted the one character, inflated crystalliferous cells, in determining the affinities of the Rumanian wood.

We do not consider the Yellowstone wood to be structurally equivalent to extant *Zelkova*, but for the three reasons listed below we name it a species of *Zelkovoxylon*, implying some, but not complete, resemblance to extant *Zelkova*. First, ring porosity in the Ulmaceae is, at times, under environmental control, and pore distribution is affected by the degree to which the ring porous condition is expressed. Pore distribution is variable within a genus because of this. Second, the Yellowstone wood has inflated crystalliferous ray cells, a feature unique to *Zelkova*. Third, there is a precedent for assigning the name *Zelkovoxylon* to woods with the combination of features found in the fossil.

There are three species of fossil wood which are very similar to *Zelkova*, as they are ring porous with a narrow, well-defined earlywood pore zone. These are *Zelkova zelkoviiformis* (Watari) Watari (1941, 1952) and *Z. wakimizui* (Watari) Watari (1948, 1952) from the Miocene of Japan, and *Zelkovoxylon yatsenkokhmelskyi* Greguss (1969) from the Miocene of Hungary. All three are younger than the two semi-ring porous species of *Zelkovoxylon*.

At present, the genus *Zelkova* is comprised of six or seven species which are distributed in the eastern Mediterranean, the Caucasus, and eastern Asia (Willis, 1973).

DISCUSSION

The ten species of fossil wood described in this paper represent a combination of so-called temperate and paratropical forms, as do the eight species described in our first paper (Wheeler, Scott, & Barghoorn, 1977). Two of the woods, *Cyrilloxylon eocenicum* and *Prunus gummosa*, have structural features (semi-ring porosity and spiral thickenings, respectively) which are generally found in the extant representatives that grow at higher latitudes. In contrast, *Turpinia lamarensis* has indistinct growth rings, a character considered to be indicative of more tropical conditions.

Zelkovoxylon occidentale, a wood that is intermediate in structure between two well-defined extant genera (*Zelkova* and *Celtis*), differs from the present-day *Zelkova* in degree of ring porosity and pore distribution, the

latter a feature affected by the degree of ring porosity. The ring porous condition in the Ulmaceae is believed to be a specialization developed in response to a seasonal temperate environment. The absence of ring porosity in this specimen may reflect the absence of such an environment. This is consistent with the subtropical climatic conditions already inferred for the Yellowstone fossil forests (Dorf, 1960, 1964) and the near-tropical climate of the nearby Kisinger Lakes flora of similar age to the Yellowstone flora (MacGinitie, 1974).

MacGinitie (1974) has commented on the lack of similarity of the Yellowstone leaf and Kisinger Lakes floras. The Kisinger Lakes flora is approximately 80 miles southeast of the Yellowstone flora, and the two are of similar age. The Kisinger Lakes flora has a "distinct tropical American aspect" and is apparently unlike the older, early Eocene floras of the Rocky Mountains which appear to have relationships to the evergreen broad-leaved and mixed mesophytic forest types. In contrast, the Yellowstone fossil flora, as presently known, does not appear to have a strong relationship to the Neotropics. None of the 18 species of wood we have described to date indicates such affinities, and many (*Quercinium*, *Pterocaryoxylon*, *Myrica*, *Nyssa*, and *Prunus*) are related to extant genera which grow in the evergreen sclerophyllous broad-leaved and/or the mixed mesophytic forest types. More detailed comparison of the Yellowstone flora with other Tertiary floras of the Rocky Mountains will be reserved for our third and final paper.

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EXPLANATION OF PLATES

PLATE I

FIGURES 1-3. *Rhus crystallifera*, sp. nov.: 1, transverse section, $\times 40$; 2, intervascular pitting, $\times 200$; 3, tangential section showing septate fibers and rays with crystalliferous cells, $\times 50$. FIGURES 4-7. *Cyrilloxylon eocenicum*, sp. nov.: 4, transverse section, $\times 45$; 5, scalariform perforation plate, $\times 140$; 6, opposite and scalariform intervascular pitting, $\times 140$; 7, tangential section, $\times 60$. FIGURE 8. *Quercinium amethystianum*, sp. nov.: transverse section, note abundant parenchyma, $\times 16$.

PLATE II

FIGURE 9. *Quercinium amethystianum*, sp. nov.: transverse section, $\times 50$. FIGURES 10-12. *Quercinium lamarensense* Knowlton, emend. Wheeler, Scott, & Barghoorn: 10, transverse section, growth ring boundary, D-2054B-42, $\times 50$; 11, transverse section, type specimen, $\times 16$; 12, transverse section, D-2054B-42, $\times 16$. FIGURES 13-15. *Pterocaryoxylon knowltonii*, sp. nov.: 13, transverse section showing diagonal pore arrangement, $\times 25$; 14, intervascular pitting, $\times 200$; 15, tangential section, note three-seriate rays, $\times 120$.

PLATE III

FIGURES 16-19. *Myrica absarokensis*, sp. nov.: 16, transverse section, $\times 80$; 17, tangential section, note crystalliferous parenchyma strands, $\times 120$; 18, scalariform perforation plate, $\times 300$; 19, vessel to ray parenchyma pitting, $\times 300$. FIGURES 20-23. *Nyssoxylon saximontanum*, sp. nov.: 20, transverse section, $\times 50$; 21, opposite-transitional intervascular pitting, $\times 220$; 22, scalariform perforation plate, $\times 375$; 23, tangential section, note composite rays, $\times 100$. FIGURE 24. *Prunus gummosa*, comb. nov.: tangential section, $\times 80$.

PLATE IV

FIGURES 25-27. *Prunus gummosa*, comb. nov.: 25, transverse section showing traumatic gum canals, $\times 40$; 26, spiral thickenings in small vessel element, $\times 100$; 27, simple perforation plate and vessel to ray parenchyma pitting, $\times 220$. FIGURES 28-32. *Turpinia lamarensense*, sp. nov.: 28, transverse section, $\times 60$; 29, tangential section, $\times 50$; 30, opposite intervascular pitting, $\times 300$; 31, scalariform perforation plate, $\times 220$; 32, vessel to ray parenchyma pitting, $\times 220$.

PLATE V

FIGURES 33-37. *Zelkovoxylen occidentale*, sp. nov.: 33, transverse section, note semi-ring porous condition, $\times 40$; 34, simple perforation plate, $\times 150$; 35, spiral thickening in small tracheary element, $\times 150$; 36, tangential section, $\times 50$; 37, tangential section showing crystalliferous marginal ray cell, $\times 180$.









